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EFFECTS OF MEDIA WITH LOW SILICIC ACID CONCENTRATIONS ON TOOTH FORMATION IN *ACARTIA TONSA* DANA (COPEPODA, CALANOIDA)

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Many calanoid copepods, the dominant herbivores in marine pelagic habitats, have elaborate siliceous teeth set in sockets on the mandibular gnathobase (Beklemishev, 1954, 1959; Sullivan *et al.*, 1975; Vyshkvartseva, 1972). The existence of these siliceous teeth raises the possibility that silicon availability is important for copepod survival, growth, or at least tooth formation. Silicic acid is present in concentrations of 150–175 μM at depth in the Pacific and Indian Oceans and of 40–50 μM in most of the Atlantic Ocean (Armstrong, 1965). However, surface layers of such huge oligotrophic regions as the Sargasso Sea (Menzel and Ryther, 1960) and Central Pacific gyre (SIO Ref. 67–5, 1967) become depleted seasonally to levels as low as 0.3 μM. These levels inhibit diatom growth even in the presence of an excess of other nutrients (Paasche, 1973a; Guillard *et al.*, 1973; Harrison *et al.*, 1976). Therefore, it is possible that other organisms with siliceous parts are inhibited by low silicic acid concentrations as well. If low silicic acid concentration at levels that occur in nature directly inhibits copepod development, then its role in the interaction of phytoplankton and herbivorous zooplankton is complex and requires evaluation.

We have conducted a first study of this possibility, employing the neritic copepod species *Acartia tonsa* Dana. This form is abundant in the waters around Woods Hole from early summer to early fall. It has three siliceous teeth: a curving spine on the ventral end of the tooth list (V), a heavy crown with four rounded points in the center (C_1), and a small bifurcate tooth just to right of center (C_2). The normal form of these teeth is shown in Figure 1. *Acartia tonsa* has been reared by Zillioux and Wilson (1966), Heinle (1969), and others. It tolerates a wide range of food mixtures, container sizes, salinities, and contaminants. We reared *A. tonsa* in media of low silicic acid concentration, trying to demonstrate the level at which development or tooth formation is inhibited.

Materials and Methods

Our experimental sequence is shown in Table I. Low silicate media (LSM) were prepared from 1) Sargasso Sea surface water (1.56 μM reactive silicate), and 2) various lots of Vineyard Sound, MA, surface water (1.26–1.56 μM reactive silicate). Water was "stripped" of silicate by growing either *Thalassiosira pseudonana* (Hustedt) Hasle and Heimdal (clone 3H, method of Guillard *et al.*, 1973) or *Phaeodactylum tricornutum* Bohlin (clone Pet Pd, method of D'Elia *et al.*, 1979) in 15- to 18-l lots enriched with nitrate, phosphate, vitamins, and trace metals to f/2 level (Guillard and Ryther, 1962). Incubation was in polyethylene bags ('Cubitainers') under four Sylvania cool white fluorescent lamps on

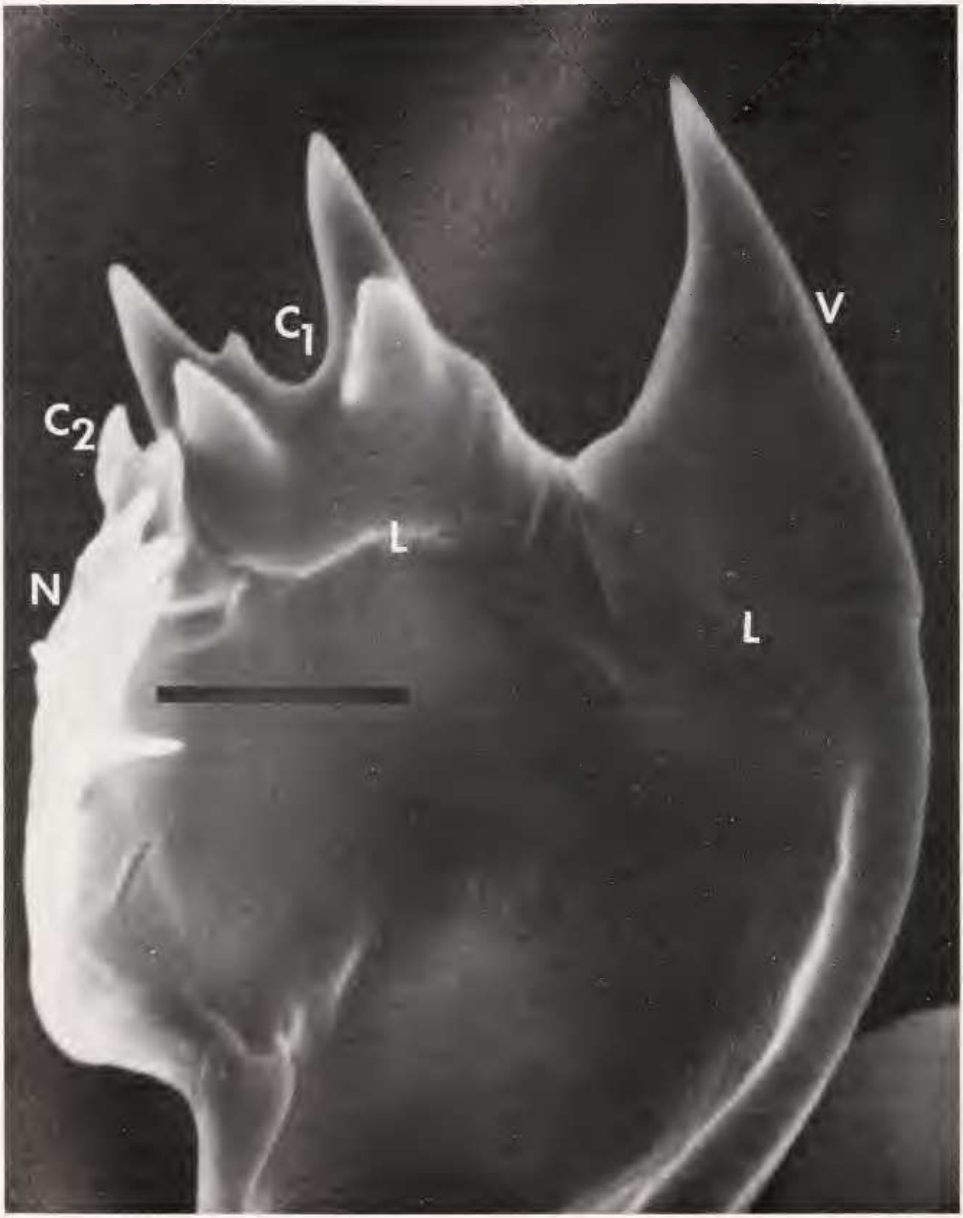
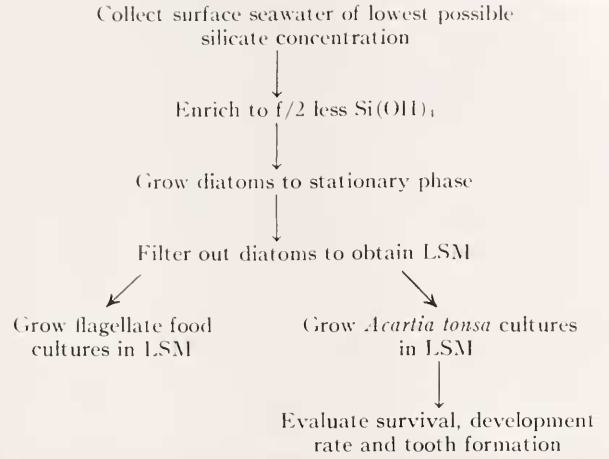


FIGURE 1. Mandibular gnathobase from adult female *Acartia tonsa* reared at 12.6 μM silicic acid (experiment I_2). The black bar represents 10 μm. Symbols: V = ventral tooth, C_1 = large central tooth, C_2 = smaller central tooth, L = limit of siliceous caps, N = nonsiliceous dorsal spine. Scanning electron micrograph by Ann Cornell-Bell (A.C.-B.) using JEOL T20 SEM at 12,500 V accelerating potential.

a 16 hr on : 8 hr off cycle. Temperature was held at 18°C. Increase in cell density of *T. pseudonana* was monitored daily by determining the *in vivo* fluorescence of the suspension with a Turner Designs fluorometer. At the end of exponential growth the cells were filtered from the water with 0.45 μm Millipore

TABLE I

Experimental sequence for producing low silicate medium (LSM) and testing its effects on tooth formation in Acartia tonsa.



HA filters using plastic filter holders and flasks. Vacuum was limited to 30 mm Hg. Silicic acid concentration in the LSM was determined as "reactive silicate" by the acid molybdate method (Strickland and Parsons, 1972).

P. tricornutum cells were removed when reactive silicate was substantially depleted. This occurred at a high cell density, though less than that at stationary phase. Stripping with *P. tricornutum* produced LSM with 0.08 μM silicic acid. However, this medium was immediately toxic to all three of the food plants used in the copepod rearing. It produced cell lysis. Its pH was found to be 9.5, presumably because of a basic extracellular product of the algae. Vigorous bubbling for several hours with CO_2, reducing the pH to 6.2, followed by bubbling with cotton filtered air raised the pH back to 7.5, removed this toxicity, and increased the silicic acid concentration only slightly. All the food plants and *A. tonsa* grew normally in the LSM treated in this manner. The toxicity is presumably due simply to the high pH, not to the specific base involved. No such effects were noted for LSM produced with *T. pseudonana*, which did not reach such high cell densities and presumably produced less extracellular material.

Three species of flagellated phytoplankton were grown in LSM to serve as food for *A. tonsa* cultures. These were *Isochrysis galbana* Parke (clone ISO), *Dunaliella tertiolecta* Butcher (clone DUN), and *Prorocentrum* sp. (clone EXUV). Each 3–4 days new cultures of each species were started in 450 ml of LSM.

Acartia tonsa was netted from Vineyard Sound on several occasions and placed in cultures by pipetting ten females and four males into 350 ml of water. A mixture of food was added to produce a final total of about 150,000 cells/ml in a volume of 500 ml. Experimental rearing in LSM was done with groups of eggs or very early nauplii produced over 2–3 days in these stock cultures. Some second generation young were used. Each culture used as a source of animals was poured through a 53 μm mesh strainer, rinsed with LSM, and transferred to LSM in a plastic petri dish. Nauplii or eggs were counted under a dissecting microscope

TABLE II

Details of experiments. Replicates have been ordered by subscripts to place similar final silicate concentrations together. Jaws from 15 or more individuals were evaluated from each replicate series, except O, P, and Q where the number of adults and late copepodites was small. "Most" implies approximately 90%.

A. Experiment 1. Sargasso Sea water; 34.5‰ salinity; initially 1.56 μM $Si(OH)_4$; LSM produced with *Thalassiosira pseudonana*; started 20 July; terminated 27 July, 1979; nauplii (N) and copepodites (C) came from different stock containers and were of various ages.

Replicate no.	Starting $[Si(OH)_4]^{-}$ μM	Animals	Survivors M	Survivors F	Survivors C	Final $[Si(OH)_4]^{-}$ μM	Result
A_1	0.40 μM LSM	30 N_1 to N_5	4	5	14	0.90	Most jaws with normal teeth, both V and C_1
A_2		40 N_1 to N_5	9	5	9	0.98	
A_3		13 small C, a few N	7	6	4	0.82	
B_1	Control 1: addition to LSM to make 1.5 μM	30 N_1 & N_2		2	19	1.44	Most jaws with normal teeth
B_2		50 N_1 & N_2			46	1.31	
B_3		30 N_1 & N_2			26	—	
C_1	Control 2: unstripped Vineyard Sound water, 1.6 μM	40 N_1 & N_2			35	3.52	Most jaws with normal teeth
C_2		40 N_1 & N_2			30	—	
C_3		42 N_1 & N_2			1	—	

TABLE II—*Continued*

B. Experiment 2. Vineyard Sound water; 33‰ salinity; initially 1.69 μM $Si(OH)_4$; LSM produced with *Thalassiosira pseudonana*; started 6 August; water changed in replicates with subscripts 1–3 14 August; terminated 18 August, 1979. H, J, and K from one stock, I from another.

Replicate no.	Starting $[Si(OH)_4]$ μM	Animals	Survivors			1 week $[Si(OH)_4]$	Final $[Si(OH)_4]$ μM	Result
			M	F	C			
H_1		30 N	3	13	1	0.23	0.18	
H_2		30 N_1 & N_2	5	15	2	0.33	0.19	Most jaws with substantial reduction
H_3	0.13-LSM	30 N_1 & N_2	1	8	1	0.18	0.22	of V and/or C_1. See Fig. 2.
H_4		30 N_1 & N_2	2	12		—	0.26	
H_5		30 N_1 & N_2	4	16	2	—	1.57	Most jaws with normal teeth
I_1		30 eggs	1	7	2	0.32	0.27	
I_2		30 eggs	1	1	10	0.18	0.21	Most jaws with substantial reduction
I_3	0.13-LSM	30 eggs		12	3	0.33	0.20	of V and/or C. See Figs. 3 and
I_4		30 eggs	3	14	5	—	0.72	5A. Fig. 5B shows exception.
I_5		30 eggs	5	12	5	—	1.27	About half of jaws with some reduction of V or C_1.
J_1		30 N_1 & N_2	3	10	3	6.43	10.21	
J_2	Control 1:	30 N_1 & N_2	2	10		6.93	12.55	
J_3	addition to LSM	30 N_1 & N_2	3	7	3	5.91	11.65	Most jaws with normal teeth.
J_4	to make *ca.* 6 μM	30 N_1 & N_2	2	8	7	—	6.32	See Fig. 1.
J_5		30 N_1 & N_2	3	14		—	11.02	
K_1	Control 2:	30 N_1 & N_2		2	11	2.94	1.90	
K_2	unstripped	30 N_1 & N_2	1	1	8	3.11	2.38	
K_3	Vineyard Sound	30 N_1 & N_2			12	3.11	2.59	Most jaws with normal teeth.
K_4	water, 1.7 μM	30 N_1 & N_2		1	15	—	10.93	
K_5		no count, N_1 & N_2		5	28	—	16.15	

TABLE II—*Continued*

C. Experiment 3. Vineyard Sound water; 33‰ salinity; initially 1.49 μM $Si(OH)_4$; LSM produced with *Phaeodactylum tricornutum*; started 13 August; terminated 24 August 1979; L, M, N in 130 ml; O, P, Q in 400 ml polycarbonate bottles.

Replicate no.	Starting $[Si(OH)_4]^{-}$ μM	Animals	Survivors			Final $[Si(OH)_4]^{-}$ μM	Result
			M	F	C		
L_1		30 N_1 & N_2	3	1	21	0.22	All adult and most copepodite jaws with substantial reduction of V and/or C_1.
L_2		30 N_1 & N_2	3	2	10	0.21	
L_3	0.06-LSM	30 N_1 & N_2	2	1	16	0.39	
L_4		30 N_1 & N_2			3	0.47	About half of jaws with some reduction of V or C_1, in no case both.
L_5		30 N_1 & N_2	2		28	0.69	
M_1		30 N_1 & N_2	1	1	16	7.17	
M_2	Control 1:	30 N_1 & N_2		8	29	—	
M_3	addition to LSM	30 N_1 & N_2	2	2	16	5.90	Most jaws with normal teeth.
M_4	to make *ca.* 5 μM	30 N_1 & N_2	3	3	15	—	
M_5		30 N_1 & N_2		4	15	—	
N_1	Control 2:	30 N_1 & N_2	1	5	19	3.15	
N_2	unstripped	30 N_1 & N_2	2	1	19	—	
N_3	Vineyard Sound	30 N_1 & N_2	1	5	15	4.31	Most jaws with normal teeth.
N_4	water, 1.5 μM	30 N_1 & N_2	2	2	23	—	
N_5		30 N_1 & N_2	4	3	19	—	
O_1		30 eggs			8	0.16	
O_2	0.06-LSM	30 N_1 & N_2	1	3	12	0.21	Most jaws with substantial reduction of V and/or C_1. See Fig. 4.
O_3		30 eggs			3	0.26	
P_1	Control 1:	30 N_1 & N_2		2	11	11.2	
P_2	addition to LSM	30 eggs			4	—	Most jaws with normal teeth.
P_3	to make *ca.* 10 μM	30 eggs	none			—	
Q_1	Control 2:	30 N_1 & N_2		2	12	—	
Q_2	unstripped	30 eggs			7	4.25	Most jaws with normal teeth.
Q_3	Vineyard Sound water, 1.5 μM	30 eggs	1	1	19	—	

as they entered a small pipette and were placed in polymethyl pentene beakers of LSM. These young were fed LSM food. Total cell density was, again, about 150,000 cells/ml. Experiments were done in 500 and 130 ml volumes. One experiment was run in polycarbonate bottles. In some cases the LSM was changed after 1 week. In others development was completed in the initial medium. One set of experimental control animals was reared in LSM with addition of dissolved sodium metasilicate to approximately f/4 levels to test the direct effect of resupplying silicic acid. Another set was reared in unstripped Sargasso Sea or Vineyard Sound water to test the possibility of adverse effects of the stripping process on water quality. Reactive silicate in the water from all containers was measured at the end of the development period.

Results

Table II lists the completed experiments and their results. Initial silicic acid concentrations in LSM were as low as 0.06 μM. In all cases, concentrations increased substantially during the experimental period. The lowest level after rearing was complete was 0.18 μM. There are two likely sources for this silicate: dissolution of bits of diatom silica which passed the filters used in producing the LSM, and dust. Since reactive silicate did not increase in stock containers of LSM, dust is the more probable source.

Specimens of *Acartia tonsa* survived as well in LSM as in the controls, and developed at normal rates. Several control groups lagged behind the LSM groups in development. This is probably not attributable to treatment differences, but to use of different stocks in establishing the groups. There were small variations in age at the start, and since there were different parents, the groups presumably had somewhat different inherent development rates. This is particularly evident in comparison of the I replicates, which started the experimental period as eggs, with the J replicates, which were early nauplii at the start.

Copepodites and adults of *Acartia tonsa* formed teeth at all of the silicic acid levels tested. However, typical specimens from low silicic-acid levels had teeth much lower in relief than those from high silicic-acid levels. This reduction was most evident in specimens from the 0.18 to 0.3 μM concentrations. Most teeth of specimens reared at levels of 0.8 μM and above closely resembled the teeth shown in Figure 1, which were formed at 12.6 μM. Reduction of teeth in specimens reared at low levels was variable both among individuals and among teeth on the same mandible. Various examples are shown in Figures 2, 3, and 4. There were exceptions (about 10–20%) in both directions: high teeth from specimens reared in the media lowest in silicic acid, and reduced teeth from specimens reared in intermediate levels.

In a number of cases the ventral tooth was so reduced that in the scanning electron microscope there appeared to be a hole completely through the siliceous structure to the chitin or tissue underneath. The jaw shown in Figure 2 has a hole of this kind in the low hummock at the position of the ventral tooth. Higher magnification, to 15,000 diameters, did not resolve the character of these holes any better (Fig. 2B). In fact, virtually no well-defined structure was apparent at any magnification anywhere on the surfaces of reduced teeth. The slight grooves apparent on the sides of all teeth were all that could be resolved better at high magnification (see Fig. 4B).

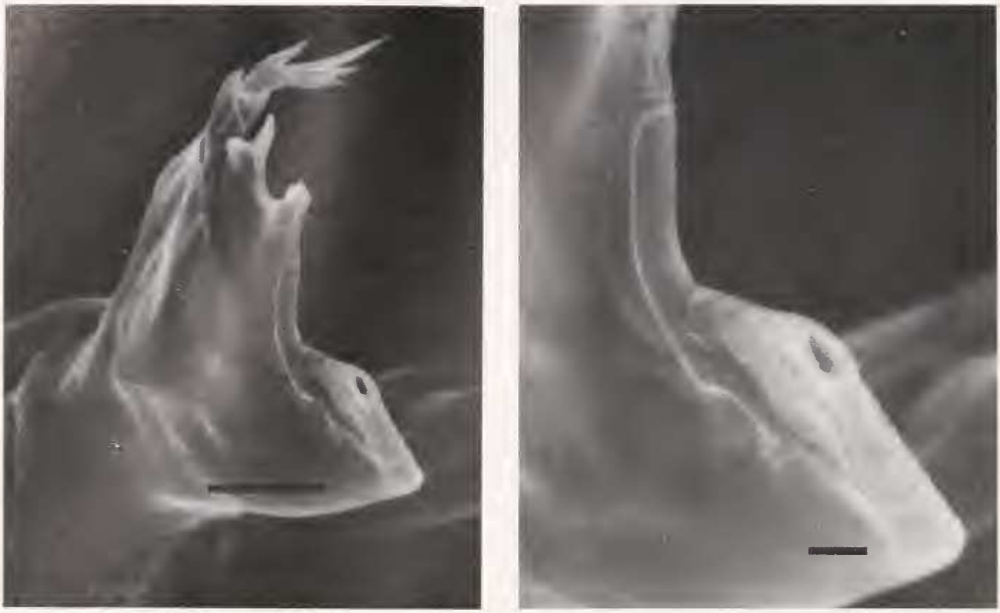


FIGURE 2. A. (Left) Mandibular gnathobase from adult female *A. tonsa* reared at 0.22 μM silicic acid (experiment H_3). The black bar represents 10 μm. The reduced ventral tooth (3 on the reduction rating scale) is on the lower right. B. (Right) Detail of same jaw shows the character of the apparent hole in the ventral tooth. The black bar represents 2.5 μm. SEM by A.C.-B.

By scanning electron microscopy, it was difficult to determine the statistical frequency of reduction. Therefore, a rating scheme was devised using light microscopy of a large sample of the jaws by four observers who did not know the origin of the jaws. The rating scale was 1 for teeth like those of Figure 1 (essentially no reduction), 2 for ventral teeth like that in Figure 3 and central teeth like that in Figure 2 (substantial reduction), and 3 for ventral teeth like those of Figure 2 and central teeth like that in Figure 3 (tooth nearly missing). The sample series was 30 right jaws from female specimens, 10 reared at each of three silicic acid levels. The results are given in Table III. Substantial reduction was found to be primarily and usually present in the specimens from the lowest silicic acid levels tested, about 0.2 μM. While different observers gave different numerical ratings, their agreement on the direction of the differences between specimens was excellent. Using mean ratings for each cell in the tables, combining the mean ratings of 2 and 3 (that is, combining all reduced teeth), and combining the mean ratings for the 0.8 and 10 μM silicic acid levels produced 2×2 contingency tables with sufficiently large expectations for statistical testing. Combining categories after the fact in this way is not strictly legitimate; however, the resulting measure of contingency of tooth reduction on low silicic acid was significant for both teeth ($\chi_1^2 > 10$, $P < 0.01$). Thus the differences between the specimen in Figure 1 and those in Figures 2, 3, and 4 are typical.

Mandibles of stage V copepodites reared in medium of 0.2 μM silicic acid concentration are shown in Figure 5. There is substantial reduction in one specimen, but not in the other. Both the reduction and its variability occur in the younger stages as well as in adults.

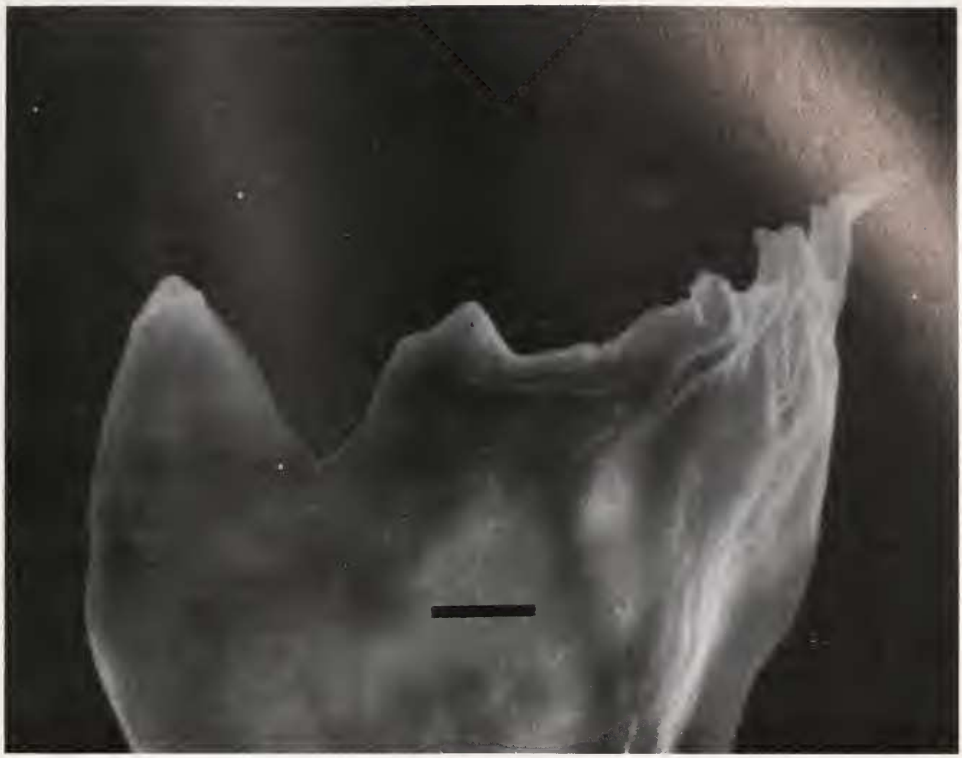


FIGURE 3. Mandibular gnathobase from adult female *Acartia tonsa* reared at 0.27 μM silicic acid (experiment K_1). The central tooth shows severe reduction (3 on the reduction rating scale). The black bar represents 5 μm. The ventral tooth is at left. SEM by Alfred H. Soeldner (A.H.S.) using ISI Mini-SEM.

DISCUSSION

Acartia tonsa successfully extracted silicic acid from concentrations in seawater as low as 0.2 μM and formed it into teeth. On the other hand those teeth were not normal. Formation of normal teeth required concentration of 0.8 μM or above. Thus we must consider both 1) the ability of copepods to draw silicon for tooth formation from lower concentrations and 2) the possible ecologic significance of low silicic acid availability.

Before we conclude that *Acartia tonsa* can draw enough silicon for tooth formation from media with low concentrations of silicic acid, several other possibilities must be considered. It could be that moderate amounts of silicon are present in seawater and LSM which do not react in the acid-molybdate analysis. Silicic acid can form polymers that do not produce the molybdate complex (Alexander, 1953), but which could possibly be used by copepods for tooth formation. However, Burton *et al.* (1970) have done a careful study of this problem. They found "no detectable amount of unreactive silicon in any of the natural water samples analyzed. Polymeric silicon added to the [sea]water samples was unstable and depolymerized completely within a few days." It seems unlikely, therefore, that copepods have any source of silicon in our experiments beside the low levels of reactive silicate which we measure. The result itself argues against another source. Normality of teeth improved with increasing reactive silicate.

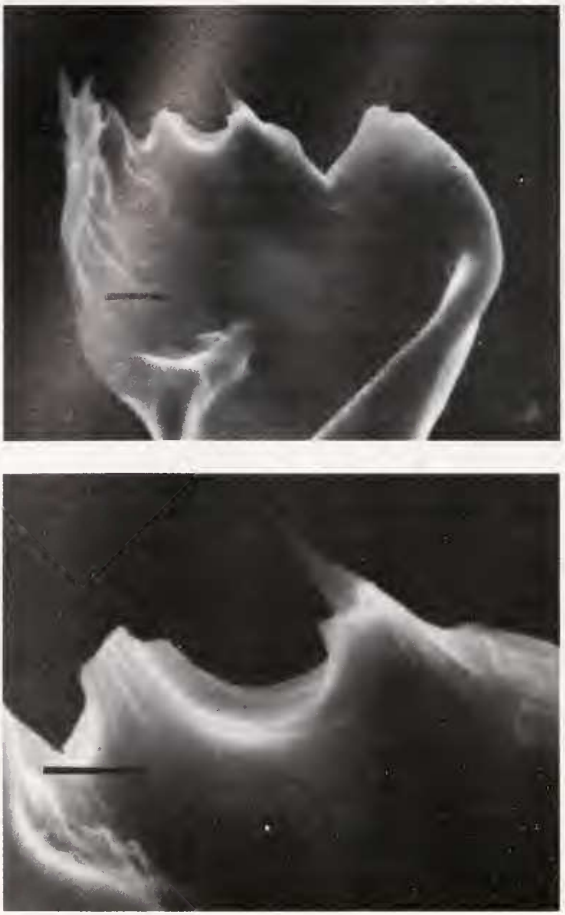


FIGURE 4. A. (Above) Mandibular gnathobase from adult female *A. tonsa* reared at 0.21 μM silicic acid (experiment O_1). Both teeth show substantial, but not severe reduction (2 on the reduction rating scale). The black bar represents 5 μm. The ventral tooth is on the right. B. (Below) Detail of central tooth shows the proximal-to-distal grooves usually on the surfaces of the teeth. The black bar represents 2.5 μm. SEM by A.H.S.

Another possibility is that *Acartia tonsa* eggs might be supplied with sufficient silicon to support tooth formation throughout the life cycle. In that case full depletion of the supply would require several generations. Some calculations show this to be unlikely. Eggs of *A. tonsa* have a diameter of 70 μm and a volume of 1.8×10^5 $\mu m^3 = 1.8 \times 10^{-10}$ liters. If silicic acid were stored in the egg at a concentration equivalent to seawater saturation (*ca.* 1600 μM), then the content of an egg would be about 2.9×10^{-7} μmoles. Plasticene models of the teeth of *A. tonsa* based on SEM pictures like Figure 1 show the volume of the teeth to be approximately $V = 7.2 \times 10^2$ μm^3, $C_1 = 1.7 \times 10^3$ μm^3, and $C_2 = 1.7 \times 10^2$ μm^3. The total tooth volume on both jaws is 5.1×10^3 μm^3. Applying the density of opal (2.1–2.3 gm cm^{-3}) this is equivalent to 1.1×10^{-8} gm. The molecular weight of solid, hydrated silica depends upon the amount of water included. For the formula $SiO_2 + 2H_2O$ the molecular weight is 96 gm $mole^{-1}$, and the amount of silica in the teeth of one adult would be about 1.1×10^{-4}

TABLE III

Results of rating by each of four observers of right jaws from female Acartia tonsa *according to the state of reduction of the ventral (V) and central (C_1) teeth. Rating was on a scale from 1 for no reduction (Fig. 1) to 3 for severe reduction. A. Raw data. The four numbers in each cell are for the four observers. B. Mean numbers of ratings. C. Means combined into 2 × 2 table.*

A.

Rating	Ventral tooth, V: Silicic acid levels—μM			Rating	Central tooth, C_1: Silicic acid levels—μM		
	Low 0.2	Interm. 0.8	High 10–12		Low 0.2	Interm. 0.8	High 10–12
1	2|2 / 2|2	8|7 / 8|8	10|10 / 9|9	1	3|2 / 2|2	9|8 / 7|8	9|8 / 10|7
2	8|8 / 1|7	2|2 / 0|1	0|0 / 1|1	2	5|4 / 8|2	1|2 / 2|2	1|2 / 0|2
3	0|0 / 7|1	0|1 / 2|1	0|0 / 0|0	3	2|4 / 0|6	0|0 / 1|0	0|0 / 0|1

B.

	Ventral tooth, V: Low	Interm.	High		Central tooth, C_1: Low	Interm.	High
1	2.00	7.75	9.50	1	2.25	8.00	8.50
2	6.00	1.25	0.50	2	4.75	1.75	1.25
3	2.00	1.00	0.00	3	3.00	0.25	0.25
Mean rating	2.00	1.33	1.05		2.08	1.23	1.18

C.

	Ventral tooth, V: Low	Int. + High		Central tooth, C_1: Low	Int. + High
1	2.00	17.25	1	2.25	16.50
2 & 3	8.00	2.75	2 & 3	7.75	3.50
	$\chi_1^2 = 12.7$			$\chi_1^2 = 11.0$	

μmoles. This is more than the maximum probable content of an egg by a factor of about 380. Additional smaller quantities would have to be present for each copepodite stage, since teeth are lost at each molt. Solid phase silica would have to be present within the egg for the entire life cycle's supply to be contained there. The weak teeth formed in our lowest reactive silicate levels also argue against this possibility. We are certain that *Acartia tonsa* can draw sufficient silicon for tooth formation from media with only slightly more than 0.2 μM silicic acid.

While we have applied a density appropriate for opal in this calculation, we have some evidence that for *Calanus* the siliceous teeth are crystalline. Fragments of tooth have irregular arrays of very sharp spots as their electron diffraction pattern. This is typical of disrupted or somewhat irregular crystals, but not of amorphous opal. Further work on the mineral character of copepod teeth is in progress.

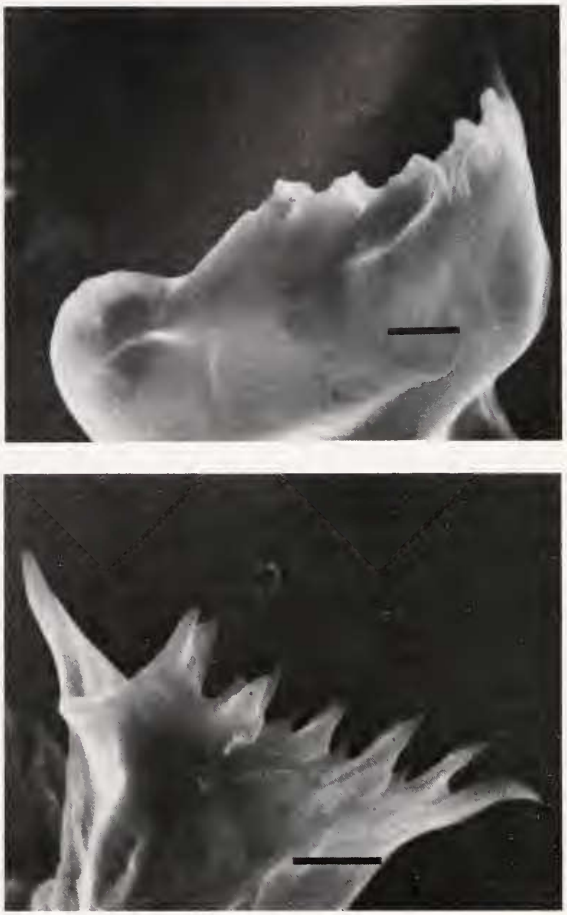


FIGURE 5. A. (Above) Mandibular gnathobase from stage V copepodite of *A. tonsa* reared at 0.21 μM silicic acid (experiment I_2). Both V and C_1 show extreme reduction. The black bar represents 5 μm. Ventral tooth is on left. B. (Below) Mandibular gnathobase from another stage V copepodite reared at 0.21 μM silicic acid (also experiment I_2). Neither V nor C_1 shows much wear. The black bar represents 5 μm. SEM by A.H.S.

A probable explanation for the reduced form of the teeth from LSM is that they have crumbled during use because of insufficient mineralization. The individuals from which all of the jaws in all of the figures came were 1–3 days past their terminal molt when they were preserved for examination. Their teeth had had some time to wear. Figure 5 shows a similar syndrome in stage V copepodites. This stage lasts approximately 1 day at 18°C, and that is apparently sufficient time for substantial wear to occur (if wear is the mechanism of reduction). Alternately, animals reared in LSM may have failed to deposit teeth of normal shape.

Silicic acid concentrations as low as 0.2 μM occur very rarely in the oceans. Thus it seems unlikely that low silicic-acid availability would ever directly inhibit *Acartia tonsa* growth, development, or tooth formation in the field. The approximately 1.5 μM levels encountered in the waters over the continental shelf of the eastern United States that are the habitat of this animal are fully sufficient. A

simple observation extends this conclusion to other copepods of pelagic habitats comparably low in silicic acid. We examined a variety of calanoid copepods from surface water at a station in the central Pacific at 30°N, 143°W (samples collected from R/V Alpha Helix in November, 1971). The ambient concentration of reactive silicate was 1.64 μM. Siliceous teeth were found in representatives of all genera studied, except *Candacia*, which has a very reduced mandible. These genera were *Calanus, Clausocalanus, Paracalanus, Scolecithrix, Euchaeta, Acartia, Centropages, Pachyptilus,* and *Pontella.* It seems very likely that the capability for making siliceous teeth at silicate levels less than 2 μM is quite general in copepods of oligotrophic habitats.

We performed our experiments with a species obviously accustomed to low silicic-acid levels. Therefore, it may be that we chose a form least likely to demonstrate an inhibition. Perhaps *Acartia clausi* Giesbrecht, which is present in Vineyard Sound from fall to spring, and which does not experience severe silicic-acid depletion in its habitat, will prove more susceptible. Thus, it is still possible that silicic acid availability plays a role in the ecologic succession of copepod species.

The flagellated forms used in our cultures surely present no severe challenge for mastication, even for individuals with the sorts of reduced teeth that develop at low silicic-acid concentration. However, extremely low silicic-acid levels are often found in the field just as a diatom bloom reaches a silicate-limited stationary phase (Dugdale and Goering, 1970; Schelske and Stoermer, 1971; Hafferty *et al.*, 1978). It is possible that copepods undergoing their last maturation molts in such conditions would find themselves unfit for sustained feeding on the abundant diatom food all about them. This could reduce their ability to produce eggs, since most copepods must eat to reproduce, and thus cause a substantial delay in reduction of the bloom. Documenting such an event in a real pelagic ecosystem would require that the investigator be on hand exactly when it occurred, something notably difficult for rare or transient phenomena of all kinds. It is also possible that sufficient silicic acid could be drawn from diatoms in the gut of maturing copeopds to form the teeth for the next phase.

Silicic acid concentrations as low as 0.2 μM, which impair tooth formation in *Acartia tonsa,* are also strongly limiting to silicic acid uptake, silica deposition, and cell division in most planktonic diatoms (Paasche, 1973a, 1973b; Guillard *et al.,* 1973; Azam, 1974; Nelson *et al.,* 1976). With the single known exception of *Phaeodactylum tricornutum* (Lewin *et al.,* 1958), the diatoms have an absolute silicon requirement for growth (Lewin, 1962). Many diatoms can take up silicic acid from concentrations of the order of 1 μM or less. This is in contrast to the silicic-acid uptake capabilities of other algae. It has recently been discovered that many planktonic algae, including *P. tricornutum* and representatives of several major taxa other than diatoms, take up and deposit substantial amounts of silicic acid when it is available (Fuhrman *et al.,* 1978; Bankston *et al.,* 1979). Kinetic experiments with *P. tricornutum* and *Platymonas* sp. (D. Nelson, unpublished data) show their uptake rates to be very low at silicic acid concentrations less than 30 μM. Their uptake systems thus have far less affinity for silicic acid than those of the silicon-requiring diatoms.

We think that this difference in affinity for silicon implies a substantially greater expense in metabolic energy or molecular complexity for systems with high affinity. Only those organisms that strictly require silicon for life meet this expense. The comparability of the silicic acid affinity of *Acartia tonsa* to that of

diatoms, in which it is an absolute necessity, thus argues that sound teeth are vitally important for survival in this copepod.

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Summary

Acartia tonsa Dana can extract sufficient silicon for formation of siliceous teeth from media with concentrations of silicic acid as low as 0.2 μM. Low silicate media were produced by growing diatoms in seawater collected from oligotrophic habitats and enriched with nutrients other than silicic acid, then removing them by filtration when they reached a silicic acid-limited stationary phase. Most teeth formed by *A. tonsa* in 0.2 μM medium were greatly reduced in profile, probably by increased effects of wear on insufficiently mineralized teeth. Teeth formed at silicic acid levels comparable to those in the field habitat of the copepod (1.5 μM) were normal. The extent of this ability to remove silicon from dilute media is comparable to that of diatoms. It is unlikely that low silicate levels in the field are an important limiting factor for *A. tonsa* or other copepods normally found in oligotrophic, pelagic habitats in the sea.

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